

clefts are supplied by their respective nerves; and that the Schneiderian folds are gills.*

These conclusions, if accepted, will considerably simplify our conception of the segmentation of the vertebrate head. As there are no nerves or clefts in front of the olfactory segment, the olfactory nerve must be taken as the most anterior nerve, and the nose as the most anterior cleft. The next cleft is that in front of the maxillo-palatine arch, of which a part probably persists in the adult as the lachrymal duct: the segmental nerve corresponding to this cleft is the *third*, or oculomotor nerve. Next comes the mouth cleft, supplied by the *fifth*, or trigeminal, nerve; and then in succession the clefts supplied by the facial, glossopharyngeal, and pneumogastric nerves. This view of the constitution of the vertebrate head is found to accord well with the later researches of Professor Parker on the morphology of the skeletal elements of the head.

Some at least of the labial cartilages will probably prove, on this view, to be homologues of the extrabranchials, a comparison that has already been made by Professor Parker.†

If the olfactory organs are visceral clefts, they must originally have communicated with the mouth cavity. Indications of a former connexion of this kind are by no means wanting; thus in salmon embryos the alimentary canal extends forwards, so as to underlie the nasal sacs: as development proceeds, this anterior prolongation of the mouth cavity gradually shrinks; it persists for a short time as a pair of cæcal diverticula, which ultimately disappear altogether.

In conclusion, it may be noted that the Schneiderian folds afford an instance, on the theory here maintained, of structures originally hypoblastic in nature becoming, from changed circumstances, epiblastic.

II. "On the Development of the Skull and its Nerves in the Green Turtle (*Chelone midas*), with Remarks on the Segmentation seen in the Skull of various types." By Professor W. K. PARKER, F.R.S. Received February 3, 1879.

In the first paper on the development of the skull of the Vertebrata, published in "Phil. Trans.," I figured and described certain modifications of the skull in the embryos of the African ostrich, which have only received their explanation lately, and this has become possible through what I see in the embryos of the green turtle.

For these embryos I am indebted to two of our Fellows, namely,

* Cf. Dohrn, "Ursprung der Wirbelthiere," p. 23.

† "Proc. Zool. Soc.," vol. x, part iv, 1878, p. 212.

Sir Wyville Thomson and Mr. H. N. Moseley; the latter (who made the collection in the Island of Ascension), sending me the smaller specimens, and the former the ripe, and nearly ripe young.

Through the liberality and kindness of these gentlemen, I am put in possession of an invaluable series of specimens, several dozens in number; the smallest being only half an inch long measured along its curve.

Sir Wyville Thomson, having accepted my offer of the memoir I am preparing on this type of reptile for the "Challenger" Series of papers, I am anxious to lay before the Royal Society some at least of the results which I have obtained; so that there may be a connexion kept up between my papers, and this slow ingathering of results be garnered in known places, for the benefit of those who will sift and use them.

I have for many years been familiar with the existence of both paired and unpaired elements in the spine and hinder part of the skull: and also with the *three* cartilages that build up the fore part of the chondro-cranium.

My attention, however, having been directed most to the symmetrical *pro-chordal* bands,—the middle and fore part of the trabeculæ cranii,—the anterior azygous cartilage, although always before my eyes, has never, until lately, received the attention it deserves.

In my first paper (on the skull of the ostrich tribe) I held views with regard to the trabeculæ which I hold now; but there has been an intermediate period in which I have fallen into, what I must now consider to be a serious error.

This error lay in the placing, both by Professor Huxley and myself, of the trabeculæ cranii in the category of visceral arches.

Both of us have known for many years that the hinder part of the trabeculæ of the newt are *para-chordal*, and I more recently discovered that the hinder part of the basi-cranial plate is developed separately in the Amphibia.

Professor Huxley restricts the term "*para-chordal*" to these hinder plates; I am satisfied that the term must have a wider application.

Nevertheless, what the Selachians, and all types above the Ichthyopsida show, satisfies me that Rathke was right in considering the trabeculæ to be mere continuations of the moieties of the basal plate, or "*investing mass*."

I quite agree with Mr. Balfour in looking upon the whole of these tracts, right and left, to be the undivided representatives of the paired neural arches of the spinal region, where, as a rule, they are distinct from each other, and are developed between the spinal nerves, being inter-segmental.

I am satisfied that dying out of the notochord in front does not affect the real nature of the *pro-chordal* tracts.

Until I understood the development of the pituitary body, its rela-

tion to the notochord was considered by me to be that of direct obstruction to the forward growth of that rod.

I now, see, however, that this azygous structure, the true skeletal axis, which is early separated from the hypoblast, begins to starve at its fore end, before the pituitary body is formed.

The main part of the hypoblast, as a rule, is arrested just behind the oral involution; and above that point the notochord ceases to grow.

At first, as Mr. Balfour shows, this rod is hooked downwards in front, for it follows exactly the curve of the mid-brain.

There is, however, at the time of its arrest, no physical obstacle to stop its growth still further forwards beneath the fore-brain, to the utmost limit of the frontal wall of the embryo.

Thus the primary skeletal axis stops and shrinks by what may be called an anticipation of the obstructing wall that will be.

Here is something in morphology resembling hereditary instinct in zoology.

The segmentation of the embryo is at first altogether that which is seen in the somatomes, and after these have become converted into the muscle-plates a new alternating segmentation takes place, so that the short muscular bands can work and produce the vermicular contractions of the embryo.

The tissue which becomes the vertebræ is primarily marked out into serial parts in conformity with the segmental cell masses that form the muscle-plates.

Very soon, however, a new segmentation takes place, and the primordial vertebræ are intermediate to the muscular masses.

This secondary, intercalary vertebrate segmentation is very slightly developed in the head.

For a good while in all the Vertebrates, and permanently in some, the mesoblastic sheath of the notochord becomes a continuous cartilage; in all but the lower forms this undergoes segmentation to form the "bodies" of the vertebræ.

In the head, as a rule, this second sheath of the notochord is but little developed, and has a very slight degree of separateness from the investing paired cartilages—para-chordals, and hinder part of the trabeculæ.

In the Selachians, however, it is well developed, and in them the distinction between head and body by means of the occipito-atlantal articulation is late; in some Batrachians, notably in the huge tadpoles of *Pseudis paradoxa*, before the limbs are grown, this cartilaginous sheath of the notochord is large and thick.

The distinction between the hind and fore parts of the skull is greater by far than the distinction between the vertebral column and the hind part of the head.

For this latter region has, in common with the spine, the notochord, its mesoblastic sheath, paired neural and hæmal elements, besides a hypoblastic lining to the digestive tube beneath.

Moreover, there is a great tendency to produce vertebræ in the hind part of the head in some Vertebrata; in several of the Urodelous Amphibia there are three rudimentary vertebræ in front of the "atlas."

Thus the scant growth of the hypoblast in the cephalic region of the blastoderm, would appear to be one of the causes of the extreme modification of the head as compared with the spinal column.*

We shall have made a great stroke in embryology when we have explained the peculiar behaviour of the epiblastic covering of the fore-part of the head.

There, the oral involution, which is formed from epiblast, turns inwards and upwards into the fore-part of the hollow under the mid-brain, and grafts itself upon the back of the down-turned fore-brain, itself of epiblastic origin; thus the pituitary body is formed.

In all available interspaces the mesoblast of the fore half of the head grows in and forms the supporting structures, and the vascular supply.

But now there arises this question—are the mesoblastic structures of the cranium in the *pro*-chordal region perfectly homologous with those in the *para*-chordal, whether cephalic or spinal?

In endeavouring to answer this question, I must return to the point at which I started, where it was mentioned that there existed an unpaired *pro*-chordal cartilage between the symmetrical trabeculæ.

This, in the fore-part of the chondro-cranium, is a familiar part—pre-nasal rostrum ("Ostrich's Skull," Plate 7, *p*, *n*); its largest development is in the skate, saw-fish, and whale.

But the perpendicular ethmoid and septum nasi are, in reality, other parts of the same azygous cartilage (see "Frog's Skull," Plate 6, figs. 9, 10); in the Batrachia I have studied the development of this median part in a large number, both of individuals and species.

But its real character is best seen in my *second* and *third* stages of the embryos of *Chelone midas*; these measured along their curves are respectively two-thirds of an inch and one inch and a quarter in length.

In the younger of these the trabeculæ are like those of the frog and Selachian, but they stop short and end in a somewhat out-turned "cornu" behind the nasal sacs; they are flat in front and rounded behind.

* Since the above was written, Dr. Milnes Marshall has shown me that in the embryo of the salmon the hypoblast, *at first*, runs forwards to the nasal sacs, and ends in a blind cavity behind the frontal wall in the fore part of the palate. One of my own figures shows this ("Salmon's Skull," Plate 2, fig. 10); I noticed and figured this upper pre-oral recess, but could not interpret its meaning.

Between these there is another (azygous) rod; this passes between the trabeculæ behind, it lies on a lower plane, and ends where the front of the pituitary body *will be*, for this part is only forming as yet.

In front this rounded rod runs forwards to the anterior wall of the head; not so the trabeculæ, for they, unlike what is seen in the Batrachia, are behind the nasal sacs, and never pass far into that region.

In the frog, and his congeners, they form a broad floor to the nasal labyrinth.

At any earlier stage than this the notochord with at least a film of mesoblast, *ensheathing the intrinsic* sheath, might have stretched itself to the point where this pre-pituitary rod ends behind; but it took an upward course, and, following the curve of the mid-brain, turned down again, and then stopped short.

I cannot see what other explanation of this *solid rod* can be given than that it is the true homologue of the mesoblastic cartilaginous sheath of the notochord; it is solid because it has nothing to enclose.

Mr. Balfour is quite right in saying that the mesocephalic flexure is only apparently recovered from; the head, indeed, has its axis permanently shortened by this bend of the mid-brain on itself.

Indeed, the skull is shortened by this, as a dress is shortened by having a "tuck" taken up in it; or as a river shortens itself when it cuts out a new channel at the base of a sharp bend.

The "post-pituitary wall" lies in the axis of the arched space formed by the bend of the mid-brain on itself; it is extremely large in the embryo of the green turtle.

It must be considered that the *frontal wall* is not the *organic* end of the embryo, but the upper surface of that end.

The fore-brain looks directly downwards, and even a little backwards; the olfactory nerves arise from its anterior (= superior) surface, and the "infundibulum" buds out to meet the oral involution on the posterior (= inferior) surface of the fore-brain.

We thus see that the true organic *punctum terminale* must lie between these two parts, the olfactory nerve and infundibulum, and therefore it looks downwards, and a little backwards.

So when the trabeculæ cranii grow to the frontal wall they in reality turn upwards, and embrace the dorsal region of the front of the head.

Thus, it is evident that if we can trace the notochord to the back of the pituitary body, we have found it reaching, very nearly, the fore-end of the embryo.

Now, in my third stage of *Chelone midas* the notochord turns round in the post-clinoid upgrowth of the basal plate, and the sheath in its descending part becomes solid, and ends behind the lobules of the rudimentary pituitary body as a tear-shaped drop or lump of cartilage.

If the head had been straight, this drop of cartilage would have reached its fore-end directly below the *first nerves*.

I shall return to this part of the subject in the latter half of my paper.

The visceral or inferior arches of the head are as diverse from the costal arches as the axial parts of the head are from those of the body.

That splitting of the mesoblast, which forms the "body-cavity," runs high up into the muscle-plates; but this upper part of the cavity closes again, whilst, below, the ventral wall is permanently divided into "splanchnopleure" and "somatopleure."

I have corroborated Mr. Balfour's account of the extension of this cavity into the head of the embryo of the Selachians by demonstrating it in the head of the embryo lizard and turtle.

To me this "head cavity" appears to be the equivalent of the temporary upper part of the body cavity; this cephalic extension of the cavity is also temporary.

The cells lining these cavities in the head become transformed into muscular fibres.

Thus, there is a reversion of the ventral wall of the head into a generalised condition before the visceral rods are developed.

In the trunk the axial skeleton* is formed inside the upper diverticulum of the body cavity, and therefore in the *splanchnic* layer; of course the costal arches pass over the permanent body cavity into the *somatic* layer.

Mr. Balfour's view with regard to the visceral arches and branchial pouches is, that they are all formed in a tract equivalent to the somatic layer of the body.

Yet the difference between the costal and visceral arches is very great; and the fact that there are two sets of them, external and internal, separated by a large *branchial space*, does not lessen the difficulty of harmonising these two sets of arches, the costal and the visceral.

We may, however, keep the term *pleural* for both, and divide this "genus" into two "species"—visceral and costal—and the visceral into two varieties, namely, external and internal.

I suspect that there has been a *secular* differentiation of these regions, and that the order in time has been—first, "extra-branchials" round the huge branchial pharynx; then the trabeculæ as a support to the swelling neural axis; then the paired neural cartilages of the spine; after these, the intra-branchials; then the costal arches; and, last of all, the limb-girdles and limbs.

These deductions are not made at random, but by reflection upon

* See Balfour, "Elasmobranchs," p. 133.

the order of time in the appearance of these parts in the *quasi-ancient* stages of the early embryos of existing, but low, vertebrate types.

The ventral wall of the head undergoes dehiscence in *three* places, on each side, in front of the tympano-eustachian, or so-called first cleft.

The right and left clefts directly in front of that open freely into each other below; they form the angles of the opening mouth.

Another cleft, the lacrymal, is formed in the region over which the third nerve forks; this nerve, the *motor oculi*, is a true segmental nerve, but is specially devoted to the eyeball.

The eyeball forms for itself a nest above and in front of the mouth, and this cupped orbital space is permanently open antero-inferiorly.

In the turtle, at my second stage, the maxillo-palatine fold is very large, is dilated at both ends, and pinched in the middle; in the hind part there is for a time, as I have showed in the lizard, an extension of the pleuro-peritoneal cavity.

This is the only one of the *head* cavities which opens into its fellow of the opposite side; the presence of this cavity is as sure a sign of segmentation as the forking of a segmental nerve over the space in front of and above it.

The thick front part of the visceral fold between the lacrymal and nasal clefts does not acquire a cavity.

The whole of this double fold over and in front of the mouth cleft is largely aborted in the Selachians by a foregrowth of the mandibular fold; but in some sharks, as in *Notidanus*, and in all rays, a true palatine cartilage is developed in that part of the face which is between the lacrymal and nasal clefts.*

Between the lacrymal and oral clefts, and therefore between the hinder fork of the third nerve and the *true anterior* fork of the fifth nerve, a visceral cartilage appears in several types.

In *Scymnus*, among the sharks, in *Menopoma* and *Siredon*, among the Urodeles, in nearly all lizards, and in the Chelonians, a separate cartilage appears in the hinder lobe of the maxillo-palatine fold, after the disappearance of the head cavity.

In the lamprey, and the larvæ of the Batrachia, the extreme forward

* This cartilage is distinct also in all the Urodeles; and in the species of the genus *Bufo*, after metamorphosis, and in all the rest of the Batrachians as a very definite region of the *sub-ocular arch*. In the salmon, among the Teleostei, this cartilage is separately developed at first, and this is evidently the rule in the Order.

In the Siluroids (*Doras*, *Clarias*) this becomes a straight rod of bone, carrying the tentacle-bearing, minute maxillary, in front, and lying over the pterygoid, and mesopterygoid behind; with these it never unites.

In lizards, and many birds, there is a very definite palatine cartilage which appears between the lacrymal and nasal clefts; it remains cartilaginous in the former, but in many birds (*Musophaga*, *Dicholophus*, *Diomedea*, &c.) acquires its own bony centre.

extension of the dorsal part of the mandibular arch suppresses the pre-oral cartilages; in the Selachians—sharks especially—this is done by the pterygoid outgrowth of the same element.

In the first case, the whole mouth is dominated by the suctorial cartilages; in the second, the immense development of the pterygoid process of the mandibular pier, antagonising the movable lower jaw, causes the great suppression of the *proper* maxillo-palatine fold.

Whilst I consider the trabeculæ to be axial, or rather *neuro-axial*, I am very familiar with the rudiments of a visceral arch growing from their fore ends.

I first saw this in metamorphosing larvæ, and adult, bull-frogs; afterwards Professor Huxley found and described them in *Rana temporaria* ("Encyc. Brit., vol. ix, Art. *Amphibia*, p. 755). Since then, I have found them in many kinds of Batrachia; in some Urodeles; in the embryos of the dog-fish (*Scyllium canicula*); in passerine birds; and in the Mammal.

Their largest development, however, is in the "Holocephalous" fishes—*Chimaera* and *Callorhynchus*.

These three pairs of rudimentary pre-oral arches are like the first post-oral of the Mammal, non-segmented; they are sometimes direct outgrowths of, and at others are formed separately from, the basal bar (trabecular).

I cannot see that these cartilages are anything else than arrested representatives of the large, fully developed post-oral arches; they correspond, however, only with the upper or suspensorial segment.

The great difference between the head and body in existing Vertebrates is shown in every part composing these two regions.

Therefore, any impatient premature attempt to make a perfect harmony between the parts that form the axial, the neural, and the hæmal regions of each, will end in disappointment.

Embryology must show us how true is the deep, essential, primary homology of these parts; but *morphology* must come in and demonstrate the great and inherited differences, slowly arising, no doubt, that are to be seen between the two regions.

There is a real *generic* likeness between the axis, the upper and lower arches, and the overlying parts in the cranial and spinal regions; let these be computed at their true worth in any comparison of the two categories one with another.

Thus, the *divided* basi-neural regions of the body are comparable with the *continuous* basi-neural regions of the head, and the visceral arches may be likened to ribs.

The "uncinate processes" of the ribs of certain reptiles (*Hatteria* and the *Crocodilia*), and in all birds, except *Palamedea*, are comparable to the branchial "rays" of Selachians; and the overlying "extra-branchials" are not void of a true similitude to the *girdles* of

the outgrowing limbs. I suspect, indeed, that they are their true serial homologues.

In this latter case, the splitting of the mesoblasts into several strata in the throat, on the one hand, and in the thoracic and pelvic regions of the body, on the other, are strictly comparable morphological changes.

I strongly suspect that if we could bridge over the gulf between the lancelet and the lamprey, we should find in these "connecting links" that the head was not a mere repetition of the body.

Somatomes we should find; but the intercalary skeletal parts would be found, I believe, to run into each other from the first, and the basi-neural cartilages of the head might be seen, *in time*, before the distinct neural arches of the spine.

I must now recapitulate a little.

After carefully considering the views and studying the researches of Huxley, Gegenbaur, Balfour, and Milnes Marshall, I am satisfied that, in spite of the doubling up of the basis cranii, at the time of its greatest flexure, there are rudiments of *three pre-oral arches*, related to *two pre-oral clefts*, namely, the lacrymal and the nasal.

That the mouth is caused by the blending together of a right and left cleft is the view held (I find) by Dr. Allen Thomson; this view, also, is held by Dr. Dohrn. (*See "Balfour's Elasmobranchs,"* p. 15.)

The horseshoe fold of the mid-brain, the formation of the large hollow bed for the eyeball, and the special function to which the true segmental *motor oculi* nerve is confined, are all correlates of the special development of those wild branches of the trigeminal and facial nerves, namely, the ophthalmic and Vidian.

This is tantamount to saying that the hypertrophy of the first and second vesicles of the brain, and the large size of the optic vesicles which are outgrowths from the first of these, with all the enfoldings and complications necessary to complete the eyeball have, together, dominated all the surrounding parts, causing them to do many strange things, so to speak, vicariously.

Milnes Marshall finds that the olfactory nerves are solid until the seventh day of incubation in the chick; in embryos of the green turtle of the size of a horse-bean, I find the nerves still solid.

When the embryos are two or three times that size, these nerves each acquire a large cavity proximally, from the fore-wall of which the branches seem to spring.

The foremost of these branches spring from the top of the vesicle; they arose at first from the top of the fore-brain.

Both in the chick and embryo of the turtle, the fourth nerve, as soon as it can be found, runs a course so directly athwart the first branch of the fifth as to suggest its *non-segmental* nature.

The sixth nerve, or *abducens*, certainly arises from the ventral surface of the hind-brain; this being so, it manifestly corresponds to the anterior root of a spinal nerve; and as Milnes Marshall suggests, it may belong to the trigeminal, to the facial, or to both of these nerves.

If low forms should turn up, in which the optic nerves were truly segmental, and not direct vesicular outgrowths of the fore-brain, that would only affect the classification here suggested, by showing that our present Vertebrata have lost a segment through the extreme specialization of the optic nerves.

As matters stand at present, we have, then, the nasal, lacrymal, oral, tympanic, and branchial clefts; of these we see that there are three in front of the tympanic, and there may be eight behind it.

Thus we get four pre-auditory and eight post-auditory clefts, with their nerves; if we add the twelfth (hypoglossal) of the "Amniota," we have obtained signs and proofs of thirteen cranial (segmental) nerves, all of these, except the last, forking over visceral clefts, and hedged in, all but the last, by visceral bars.

The first of the bars is in front of the first or nasal cleft, the last, or thirteenth, is the hinder bar of the lamprey's branchial basket work.

Of course in this classification I do not mention, for the time, the distinction between the *deep* and *superficial* cartilages.

In the lowest kind of chondro-cranium known to us, namely, that of the sucking-fish and the larvæ of the Batrachia, the first post-oral arch is not only very largely developed, but is also carried forwards directly to the front of the head; it does not of itself form the skeleton of the oral opening, but carries the large cartilages that form the peculiar suctorial mouth.

Hence, in the lamprey and in the Batrachia, whilst they are in the larval condition, the pre-oral visceral bars are arrested in their growth; in the adult of the latter types, when the permanent mouth is formed, then two (of the three possible) visceral arches are developed.

Not only in low forms are the anterior visceral arches arrested, or even suppressed, but the visceral clefts also, in front of the mouth as well as the one immediately behind it, are often imperfectly developed, or even suppressed.

The nasal cleft does not remain open inwards until we get to the Dipnoi and Amphibia, and the lacrymal cleft not until we get to the Amniota.

No one has seen a first post-oral or tympanic cleft in the lamprey, and its second post-oral, discovered a few years ago by Professor Huxley ("Proc. Roy. Soc.," vol. xxiii, p. 129), in the larva, or *Ammocæte*, is very small, and apparently has no external opening.

In all the Urodeles, and in the lower and more generalized Anura,

the first post-oral or tympanic cleft is either suppressed or forms a very slight *inner pouch*; it never opens externally in the Anura.

In most of the Ganoids, as in the Selachians, the first post-oral cleft persists as the spiracle, but in osseous fishes it is a very temporary structure.

I have long suspected that the archaic (entomocranial) Vertebrata were often supplied with a perfect circlet of branchial filaments around their mouth.

We know the first post-oral cleft to be a branchial cleft with several branchial filaments; Dr. Milnes Marshall's researches show that the nasal folds of the embryo Selachian are developed in precisely the same manner as the external branchials of the spiracular opening.

These filaments become converted into a pseudo-branchia; the natural suggestion is that the nasal folds, having the same structure, and being formed in a homologous space, are indeed nothing more, even in the adult, than a modified pseudo-branchia.

Further Remarks on the basi-neural Plates of the Skull.

I have latterly come back to the same view as to the meaning of the "trabeculæ cranii," as was first propounded by Rathke, namely, that they are there extensions forward of the basal plates or "investing mass."

Professor Huxley's term "para-chordal" is as applicable to the hind half of the trabeculæ, in embryos of Selachians and Amphibians, as to the pair of plates behind the trabeculæ, or "para-chordals" proper.

Moreover, in several kinds of Urodeles, namely, (*Spelerpes*, *Desmognathus*, &c.,) there is a *hindmost* pair of para-chordal cartilages in front of the *functionally first* vertebra.

It behoves us, therefore, not to be led astray by mere words; I should prefer to call the paired cartilages of the notochordal region of the head *basi-neural*; this term would satisfy not only some of the best authors, such as Goette and Balfour, but it also expresses what I conceive to be the actual nature of the parts.

These right and left tracts of cartilage that form the main part of the base or skull floor, and grow, more or less, over the overgrown neural axis, are divisible into two regions, the hind region, which is *para-chordal*, and the fore-part, which is *pro-chordal*.

These essentially continuous tracts were, I suppose, developed, first, as a support to the increasing fore end of the neural axis, and from the first were not clearly divided into intercalary (inter-neural) tracts; and moreover, as I take it, they solidified earlier than the inter-neural tracts of the spinal region.

That *these latter*, even, were not always from the first developed

into separate tracts the existing *skates* and *rays* show; as the tissue became more and more solid, it became, in relation to the action of the muscle-plates, differentiated into a paired chain of pieces of solid cartilage for the *origin* and *insertion* of the segmental muscles.

The "basi-neural" tracts of the head in existing Vertebrata are developed very differently in different types, some parts forestalling others in chondrification, and yet not similarly in all.

In the Salachians (*Scyllium*, *Raia*, *Pristiurus*, see "Trans. Zool. Soc.," vol. i, Part IV, Plates 33-42) these tracts are very broad, and there are *three* regions made evident by the earlier or later time at which they become converted into hyaline cartilage.

The middle region chondrifies first; this extends from the nasal sacs to the middle of the auditory capsules, and answers to the "trabeculæ" without their "cornua."

The next tract is behind the trabeculæ; it does not end close behind the exit of the *vagus*, but runs on for a considerable distance into the spine, without any sign of segmentation.

The last to solidify its *embryonic*, into *hyaline*, cartilage, is the *inter-nasal*; this tract is, at an early stage, narrow, for the nasal sacs are immense; afterwards these structures get much further apart, and allow of the free development of the intervening cartilage.

This overshadowed, pinched tract of the skull, breaks out into three parts in front of the nasal sacs,—a pair of bilobate, "cornua trabeculæ," and the azygous "pre-nasal" rod.

That rod is the fore part of the *inter-trabecular tract*; it is but little evident between the nasal roofs, and between the eyes only forms the thinner middle part of the cranial floor.

But the azygous cartilage, behind the pituitary body, forms the undivided, secondary (mesoblastic) sheath of the notochord; in the early embryos it runs on from the pituitary space to the end of the body: afterwards, it is segmented at the occiput, and behind that region becomes segmented (more or less) into "centra."

Yet in the rays a large *post-occipital* tract is continuous, permanently; and in both rays and sharks it shows at first *signs of extensive segmentation in the head*, for the notochord at its fore end becomes "moniliform." I find *five* joints or beadings in *Pristiurus*, and *eight* in *Scyllium*.

In the Urodeles ("Skull of Urodeles," Plate 22, fig. 1, *tr*), for instance in the axolotl-embryos at the time of hatching (my *second* stage), show a pair of broad para-chordal cartilages that embrace the fore half of the relatively huge notochord. These grow in front of that rod as small rounded horns, embracing the sides of the fore-brain below.

Afterwards these rods grow up to, and then between, the nasal cap-

sules, and then spread into dilated out-turned "cornua." By that time another pair of para-chordal cartilages has appeared behind the first, and in several species of Urodeles a much smaller pair behind them. I do not find more than a very delicate layer of mesoblast sheathing, the cephalic part of the notochord; and the inter-trabecular cartilage in front of it merely fills the interspace of the trabeculæ in the nasal region; only in *Siren* and *Salamandra* do I see a short "pre-nasal" rod.

In most of these types the two last-mentioned being exceptional, the para-chordal part of the trabeculæ is absorbed, and only a selvege of the para-chordal, proper, remains inside the car-capsules, and at the occipital condyle.

In these types the basal cartilage does not grow up into the cavity of the mid-brain as a "post-clinoid" wall, but this wall is very well seen in the dog-fish (*Scyllium*).

In the Batrachia ("Anura") the trabeculæ embrace the apex of the notochord less, and develop their cornua sooner; the rest of the basal plate, behind, is somewhat later in its appearance. They have a continuous growth of the *inter-trabecular* band, which is a flat floor finishing the skull below; between the eyes, and between the nasal sacs it grows into a wall; in front, this tract fills in the angle between the trabecular cornua, and often (as in the tree-frogs) sends forth a distinct pre-nasal rod, like that of the sharks.

The Anura have a slight post-clinoid wall; their skull on the whole, *when finished*, is intermediate between that of the Selachians and the Urodeles. Goette mentions the cartilaginous sheath of the cranial notochord in *Bombinator*; I find it very massive in the larvæ of *Pseudis* (when the limbs are just appearing); but, as a rule, this sheath is very thin in tadpoles.

In Teleostei ("Salmon's Skull," Plates 1—8) the investing mass chondrifies first, and is relatively much larger than the trabeculæ: they are only *sub-distinct*, and soon coalesce; the trabeculæ grow very rapidly, so that at the time of hatching there is a very massive *pro-chordal* tract.

By the middle of the second week after hatching the *pro-chordal* tracts are quite distinct from the *para-chordal*, and lie on them obliquely.

By the middle of the first summer the tracts show, as far as I can see, no sign of their separation; but in the adult salmon the trabeculæ only reach to the front of the pituitary space, whilst the anterior half of the para-chordal cartilage receives its bony matter from their "prootics."

In the salmon the middle ethmoid is at first feebly developed, growing down, as a keel, from the "tegmen cranii;" and in the adult all we see of the *inter-trabecular* point is a short wall between the lateral

ethnoidal masses; for, further forwards, at the mid-line, there is a large cavity filled with fat.* In front the trabeculæ end in two short cornua, but there is no "pro-nasal" rod.

In the snake ("Snake's Skull," Plates 27—33) the cranial part of the notochord shortens rapidly, and is invested with a very thin secondary sheath. The trabeculæ are manifestly merely *fore-growths* of the para-chordal tracts: there is no inter-trabecular tract, and even the "septum-nasi" is formed by the two trabecular crests uniting with the inner edge of each nasal roof. The snake has a post-pituitary wall, which is well developed in all the "Sauropsida."

In the high-skulled lizards the inter-trabecular cartilage appears, and largely contributes to the formation of the partition wall in the fore part of the head; it does not, however, appear, wedging in between the trabeculæ below, as in the Chelonians, nor has it any *pre-nasal* growth in any kinds I have worked out.

But the Chelonians shed most light upon these parts, and my recent work at this type has made many things clear to me that for a long time have remained unexplained.

The segmentation of the pro-chordal from the para-chordal region is both *secondary* and *temporary*: it did not exist in my *first* stage, and had vanished in the *fourth*, namely, in embryos three-parts ripe; these, which were the size of a horse-bean (*third* stage), corresponded with what is seen in the adult salmon.

The embryos of *Struthio camelus* come very close to *Chelone* as to the invedged position of the inter-trabecular tract, which appears below, and makes the base of the orbital septum carinate.

This is not seen in the other "*Ratitæ*" nor in the "*Carinatae*;" but I find it in the ethnoidal region in the chick ("Fowl's Skull," Plate 81).

Also in having large orbito-sphenoids the African Ostrich comes nearest to *Chelone*. Neither of these types, nor the other "*Ratitæ*," show the segmentation of the perpendicular ethnoid from the septum nasi, which is constant in the "*Carinatae*," and is seen to begin in Lizards.

In Mammals (Pig's Skull, Plate 28, fig. 8), the para-chordals chondrify before the pro-chordals; the latter, however, are never separated from the former. The "inter-trabecular" wall dominates in the front of the pituitary space, but the thin, flattened, vertical trabeculæ diverge at a certain point to form the huge orbitosphenoids, exactly as in *Chelone* (Plate 33, fig. 6).

The shortening of the skull by the fold of the mid-brain, and the high post-clinoid wall growing up into the hollow, are just alike in the turtle and the pig.

* Dr. Milnes Marshall has shown me that the want of symmetry seen in my salmon embryos was artificially produced by the spirit; they should have been removed from the egg before they were preserved.

On the Organic and Actual Fore End of the Head.

When the cephalic fold of the embryo is formed, the fast-growing cerebral bulbs hang over the yolk; the brain at this stage, by its own bulk and weight, hangs down like a gourd.

Of necessity, this throws together parts that would be at some considerable distance from each other; also the *organic* end is not the *actual* end of the head, as I have mentioned before: *that* is formed by the mid-brain; the fore-brain, or terminal vesicle, looks downwards and backwards.

In this piece of morphology, as in studying the "receptacle of the fig-tree," we have to distinguish between the *apparent* apex and the *true* apex.

But if organs have to be supported, the morphological force must make good that which is thrown out of gear by this special hypertrophy of parts, and the beams and rafters must be eked out.

For this heavy nodding bend of the growing brain so doubles up the undergrowths of the skeletal rudiments, that both the paired and unpaired parts are stopped very near to the *retrol* organic apex.

Also the nasal sacs and optic vesicles, attached to, or growing from, the fore-brain, are in a new position, and not, as they should be, in the old straight line.

Indeed, the axis of these skeletons grows up far into the hollow bend of the mid-brain, and the notochord turns over somewhat, and then loses itself in the mesoblastic sheath, which gets very close to the *organic end* of the brain.

The paired tracts (para-chordals, both trabecular and post-trabecular) grow up into that hollow, and there stop; their new outgrowths (or eking out of the basi-neural tracts) begin again at the base of this ascending wall.

Also the middle (*unpaired*) part begins again directly, in *Chelone*, and in embryos (two-thirds ripe), in which the notochordal sheath was ossifying to form the beginning of the "basi-occipital" and "basi-sphenoid," the *cephalostyle* passed at once from the notochordal sheath to embrace and ossify the "inter-trabecular" bar, close below the pituitary body.

That part of the basi-sphenoid which lies in front of and below the pituitary body is formed by ossification, directly from the cephalostyle, of the unpaired solid pro-chordal tract of mesoblast; afterwards the bony matter spreads into the paired bars (trabeculæ).

But that middle bar came short of the pituitary space in the earlier stages; for there the *oral fold* grew up to graft itself upon the fore-brain, close behind (or *below*, organically), the true apex or end of the brain.

Hence we see, that if the pituitary body were formed in an *unbent*

embryo, it would be close below, and only a little behind, the fore end of the creature; in this supposed type the notochord would be only a little behind the *punctum terminale*.

Now the fore and mid brain have at present only yielded to embryologists *one pair each* of segmental nerves growing from their dorsal region; the hind brain is a *series* of enlargements.

The two great *pre-aural* segmental nerves (5th and 7th) by the overfolding of the brain, are enabled to send on to the front of the head their special branches, needed there, because of the specialization (for motion) of the *third*, and the specialization (for sensation) of the *first* nerve.

Thus these three-branched nerves have grown in harmony with the paired and unpaired *basi-neural* cartilages, and there is a due extension forward of cartilages to the partially straightened skull, and a due supply of nerves from behind.

But in spite of all the metamorphoses of these parts, neural and skeletal, if Dr. Milnes Marshall's observations (with which mine accurately accord) be true, then we still have two true segments in point of the cleft (*oral*) which is forked over by the 5th nerve. It could not be expected that the visceral arches and intervening clefts would be otherwise than greatly modified and masked in the fore part of the head, with its huge nervous centres, and highly complex organs of special sense.

The larvæ of the Amphibia, especially of the "Anura," have been very carefully studied by me, as likely to throw light upon the order of development of the cranial-facial skeleton; the lamprey, also representing those larvæ permanently, has been the subject of much thought, as a sort of practical pattern of those larvæ. In these forms the *extra-visceral* skeleton of the head is much developed, and only part of the true visceral (internal arches) appear.

For the mouth in these forms is terminal, and its skeleton is made up of *sub-cutaneous cartilages*, the serial homologues of the subcutaneous basket-work of the large respiratory pharynx of the lamprey.

In that form the only true visceral arches developed are the mandibular and the hyoid; a basal rudiment of the internal branchial arches exists as the "lingual cartilage."

The free mandible of the lamprey is packed up, and apparently functionless, close behind the postero-superior "*labial*;" the quadrate portion of the "suspensorium," is a mere point or style, with no condyle.

This suspensorium throws a fold of cartilage over the second branch of the 5th nerve and the temporal muscle; this is not the pterygoid cartilage, and is only seen in this type, in tadpoles, and in some chondrosteous Ganoids, *e.g.*, *Planirostra*, as shown by Mr. Bridge.

Also the epi-hyal is in a low state of development; there is a cerato-hyal and a basi-hyal piece, growing forward below, in front of the large lingual ("basi-branchial") cartilage.

But there is a copious growth of external cartilage both around the terminal mouth and around the huge branchial pharynx; the cranial box is at a low state of development, and the fore part of the head shows no trace of a pre-oral arch.

In tadpoles we have a very similar state of things, but there is a real ascent; the suspensorium develops a quadrate condyle, and on this the *passive* mandible is hinged.

Round the mouth, cartilages quite like those of the lamprey, are developed, but they are smaller; and there are only four bars (pouches) in the walls of the pharynx; rudiments of four *true intra-branchials* also, are developed. A fifth subcutaneous cartilage appears during metamorphosis, belonging to the mandibular arch; it becomes the cartilaginous "annulus tympanicus."

After it has appeared the "styloid cartilage" of the lamprey ("epi-hyal") is, in them, slowly developed, and becomes the "columnella auris."

Also, during metamorphosis, the rudiment of a "palatine" visceral arch appears, and in the genus *Bufo* becomes a large distinct *pre-oral* cartilage. After metamorphosis, another cartilage appears on each side, within the nasal cleft, the "pro-rhinal."

My idea of the order, *in time*, of the skeletal elements is as follows:—

First. The superficial cartilages of the mouth and respiratory pharynx.

Secondly. Basi-neural, and then, afterwards, going from them, *visceral* cartilages, in the *inner layer* of the walls of the mouth and throat.

Thirdly. After that, selection of dermal scutes, first as scales and afterwards as splint-bones ("parostoses"), to supplement, for supporting purposes, the chondro-cranium.

Fourthly. A gradual *arrest*, and then more or less of *suppression*, of the chondro-cranial parts, and the increased use of subcutaneous investing bones, at times in conjunction with remnants of the *old primary superficial* cartilages.

The development of the spine has been, I believe, a thing of *later date*; and the limb-girdles and limbs newest and latest of all.

The brain, mouth, and throat, with coiled intestines, whose outlet is very little behind the occiput, make up all that is of any consequence, in such a form as the gigantic tadpole of the paradoxical frog (*Pseudis*); whose post-cranial segments have evidently been super-additions, developed for the sake of locomotion—to form a mere swimming organ.

Behind the head, the segments for free motion cannot be moved by the developing segmental muscles until an intercalary segmentation has taken place; hence the vertebral segments which come between the "muscle-plates" and spinal nerves.

The head, eschewing such mobility, has developed an axial box for the brain, and beneath this firm structure, the mobile and distensible mouth and throat are swung.

III. "On an Extension of the Phenomena discovered by Dr. Kerr and described by him under the title of 'A New Relation between Electricity and Light.'" By J. E. H. GORDON, B.A., Assistant Sec. of the British Association. Communicated by Professor TYNDALL, F.R.S. Received February 10, 1879.

In November, 1875, Dr. Kerr announced in the "Philosophical Magazine," that he had discovered a new relation between electricity and light. He showed that when glass is subjected to an intense electrostatic stress, that a strain is produced which causes the glass to act like a crystal upon polarized light.

On Wednesday, February 5, 1879, I was working at this experiment in the Royal Institution, and endeavouring, by means of the electric light, to project the effect on a screen, in preparation for a lecture on the next day.

In the experiment as described by Dr. Kerr, and which was shown plainly on the screen, on February 6, the light is extinguished by the Nicols, and reappears when the coil is set going.

In the projection experiment a patch of moderately bright white light, about 3 inches diameter, appeared on the screen when the coil was worked. The images of the points inside the glass were about $1\frac{1}{2}$ inches apart. On Wednesday, however, the electrostatic stress was accidentally allowed to become strong enough to perforate the glass. Immediately before perforation there occurred the effects which are the subject of the present communication.

First appeared a patch of orange-brown light about 6 or 7 inches diameter. This at once resolved itself into a series of four or five irregular concentric rings dark and orange-brown, the outer one being perhaps 14 inches diameter. In about two seconds more these vanished and were succeeded by a huge black cross about 3 feet across, seen on a faintly luminous ground. The arms of the cross were along the planes of polarization, and therefore (the experiment being arranged according to Dr. Kerr's directions) were at 45° to the line of stress.